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Review article

Morpho-physiological and biochemical response of rice (*Oryza sativa* L.) to drought stress: A review

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ABSTRACT

Global food shortages are caused mainly by drought, the primary driver of yield loss in agriculture worldwide. Drought stress negatively impacts the physiological and morphological characteristics of rice (*Oryza sativa* L.), limiting the plant productivity and hence the economy of global rice production. Physiological changes due to drought stress in rice include constrained cell division and elongation, stomatal closure, loss of turgor adjustment, reduced photosynthesis, and lower yields. Morphological changes include inhibition of seed germination, reduced tillers, early maturity, and reduced biomass. In addition, drought stress leads to a metabolic alteration by increasing the buildup of reactive oxygen species, reactive stress metabolites, antioxidative enzymes, and abscisic acid. Rice tends to combat drought through three major phenomena; tolerance, avoidance, and escape. Several mitigation techniques are introduced and adapted to combat drought stress which includes choosing drought-tolerant cultivars, planting early types, maintaining adequate moisture levels, conventional breeding, molecular maintenance, and creating variants with high-yielding characteristics. This review attempts to evaluate the various morpho-physiological responses of the rice plant to drought, along with drought stress reduction techniques.

1. Introduction

Rice (*Oryza sativa* L.) needs enough water because it is a semi-aquatic plant. Drought affects rainfed ecosystems and plants at different life stages [1]. Crop growth factors are negatively impacted by drought, which reduces production. Zhang et al. [2] reported 25.4% decline in rice yield because of drought stress. Furthermore, drought during flowering time negatively impacts the overall amount of filled grain panicles [3]. Drought is typically defined using three criteria: meteorological, hydrological, and agricultural

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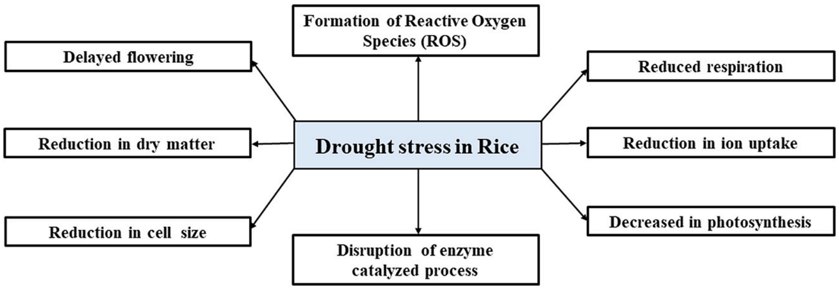

Fig. 1. Diagrammatic sketch showing the physiological effect of drought in rice.

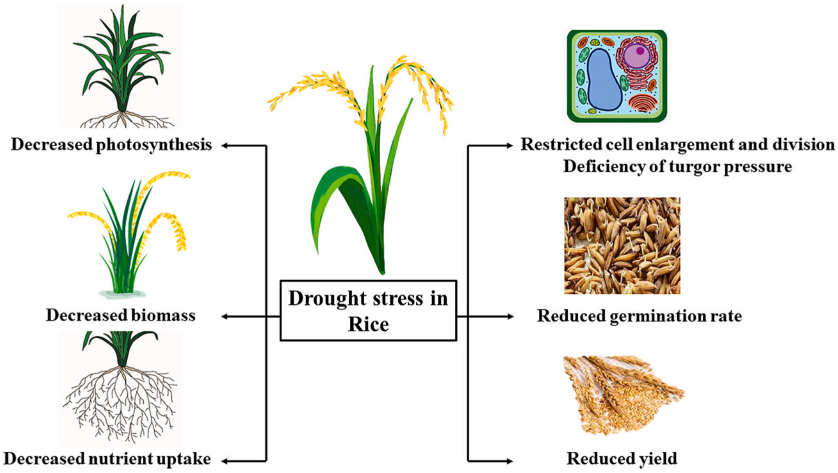

Fig. 2. Effect of drought stress at various parts of rice leading to the decline in photosynthesis, biomass, nutrients uptake, cell division, turgor pressure, and ultimately reduced yield, modified from Rasheed et al. [25].

drought [4]. It has also been identified as the main obstacle to the development of rainfed rice, influencing the crop's morpho-physio characteristics [5]. The drought affects morphological, physiological, biochemical, and molecular responses in rice plant [6]; the effect of drought stress in rice plant is shown in Fig. 1. Drought stress is characterized by decreased water content, reduced leaf water potential, turgor pressure, stomatal activity, and decreased cell expansion and proliferation. In addition, it inhibits photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutritional metabolism, stunted development, and so on, all of which contribute to reduced plant growth. Drought stress initially restricts rice plant growth by reducing cellular elongation and expansion [7], detrimentally affecting seedling development and germination [8,9], leading to reduced plant growth and development. Moreover, the impacts of drought stress on rice plants include disruption of enzyme-catalyzed processes, production of growth promoters, source-sink relationships [10].

By using techniques like breeding and Marker Assistant Selection (MAS), plant hormones like auxin, gibberellins, cytokinin, and brassinosteroids can be used to modulate drought responses. Other techniques include enhancing osmotic adjustment with potassium nutrients and osmolytes like glycine betaine, and other amino acids, polyols like sorbitol, mannitol, myo-inositol, and pinitol. Trichoderma has evolved morphological adaptations to avoid drought, physiological and biochemical adaptations to tolerate drought, and increased drought recovery mechanisms, among others, to alter its drought response [12]. The screening for rice varieties tolerant to drought is an important approach for development of drought tolerant rice varieties. The complex nature of breeding for drought-tolerant rice varieties makes it a challenging endeavor, and multigenic regulation of drought-tolerant features would be a significant research bottleneck.

The development of drought tolerant varieties may be an economical approach for boosting rice production under drought stress. The comprehensive studies on morpho-physiological responses of the rice plant to drought and drought management are limited. In this article the morpho-physiological and biochemical responses of rice to drought and their adaptations of mitigation mechanisms is discussed. The present study therefore provides the morphological and physiological characteristics of drought tolerance, and deals with drought stress reduction techniques. This review serves as useful guide for rice growers, researchers and academicians for rice production under drought stress conditions.

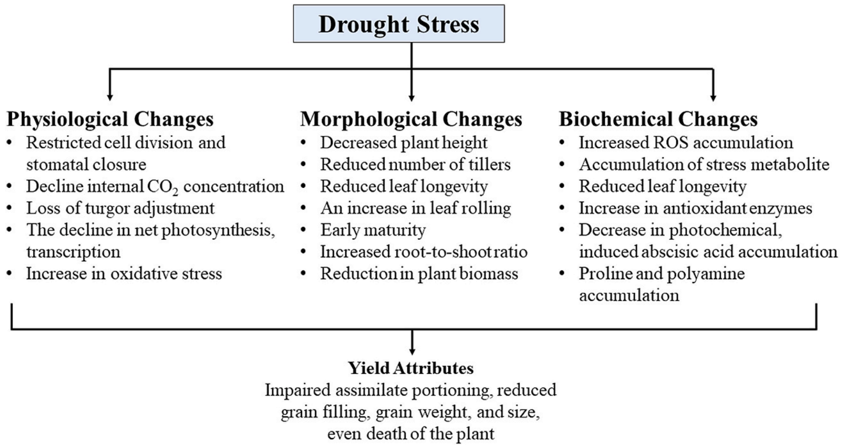

Fig. 3. Various changes brought up by drought on rice plants, modified from Oladosu et al. [10].

2. Effect of drought on the morphological parameters

Drought stress negatively impacts the general morphology of rice plants, including plant growth, plant biomass and yield, roots, and grain development. In terms of morphology, plants under water stress exhibit decreased germination, leaf size, leaf area, leaf number, biomass, cell growth, and elongation due to low or insufficient water flow onto the xylem or neighboring cell. Another apparent morphological change is leaf rolling, stomata closing, leaf tip drying, and root shortening [13]. According to several reports, water stress causes declines in plant height, leaf area, and biomass [14–16] (see Fig. 2).

The effect of drought on morphological parameters is given in Fig. 3.

3. Effect of drought on the physiological parameters

Drought stress adversely affects different physiological functions, and plants react to acclimate the unfavorable conditions. Therefore, prior to breeding programs it is crucial to improve physiological factors and processes for increased yield under drought condition [13,17,18]. Numerous physiological traits of rice are negatively impacted by water scarcity, including net photosynthetic rate, transpiration rate, stomatal conductance, water use efficiency, internal Carbon dioxide (CO_2) concentration, photosystem II (PSII) activity, relative water content, and decrease in membrane stability index decreases [13,19–21]. The physiological reactions include membrane stability and an increase in osmoprotectants [22].

Stress from drought prevents crops from producing at the threshold by changing physiological processes of plants. Drought sensitivity is correlated with physiological traits such as stomata diffusive resistance, stomata closure and opening, stomata osmotic adjustment, leaf rolling, water retention, and leaf senescence [22]. The effect of drought stress in physiology of rice is detrimental in several ways (Fig. 1). Stomata close as a result of drought stress, reducing the gas exchange. Reduced soil moisture may have resulted in lower leaf water content, causing guard cells to lose turgor pressure and, as a result reducing the size of stomatal apertures [23]. Stomata closure lowers CO_2 inflow, thus lowering photosynthetic activity, which in turn lowers metabolic activity in the plant [24].

The effect of drought on physiological parameters is given in Figs.1 and 3.

4. Biochemical responses to drought

In response to drought stress, plants accumulate organic and inorganic solutes that lower the osmotic potential to maintain cell turgor. The plant achieves osmotic adaptations by accumulating osmoprotectants such as proline, glycine betaine, and soluble sugar [26]. Protein content, profiling, and increased antioxidant activity for scavenging Reactive Oxygen Species (ROS) improve drought tolerance [11]. Other techniques include enhancing osmotic adjustment with potassium nutrients and osmolytes like glycine betaine, and other amino acids, polyols like sorbitol, mannitol, myo-inositol, and pinitol. Tissue and time-specific expression of drought-response traits, such as abscisic acid (ABA), brassinosteroids, and ethylene phytohormone pathways, improve drought response without depressing yield [18]. ROS, primarily produced in chloroplasts and to a lesser extent in mitochondria during drought stress, build up and cause oxidative stress. Singlet oxygen, superoxide anion radicals, hydroxyl radicals, and hydrogen peroxide (H_2O_2) are four main ROS molecules [27]. When exposed to oxidative stress in addition to drought, plants exhibit additional defense mechanisms to protect themselves from the cumulative effect of combined stress. Better tolerance and resistance to oxidative damage are found in plants with high induced antioxidant levels [28]. A commonly used defensive mechanism against abiotic stressors is the ROS scavenging mechanism [29]. Plants can naturally create a range of antioxidants to detoxify ROS, reducing oxidative damage and increasing drought tolerance. ROS scavengers are antioxidant enzymes such as superoxide dismutase, peroxidase, and catalase. The activity of antioxidant enzymes increases dramatically during drought stress in drought-adapted rice varieties. It creates a notable shift in the proline accumulation in certain types [16]. By balancing the osmotic potential of the cytosol with that of the vacuole and the

Table 1
Summary of the reduction in the rice yield countered during different stages.

Growth stages	Level of severeness	Yield reduction (%)	References
Vegetative stage	Severe	50.6	[39]
Vegetative stage	Moderate	21	[14]
Flowering stage	Severe	76.7–83.7	[40]
Flowering stage	Severe	>70	[41]
Flowering stage	Moderate	50	[14]
Flowering stage	Severe	63.1	[42]
Flowering stage	Severe	70	[42]
Flowering stage	Moderate	90.6	[42]
Flowering stage	Moderate	51	[43]
Flowering stage	Severe	60	[43]

environment outside the cell, the proline accumulated in plants under water stress can protect it [30]. Hence, the proline accumulation and antioxidant enzymes are linked to dry mass formation and the drought resistance of upland or drought-resistant cultivars. Tolerance to drought stress is correlated with antioxidant systems and substrates in higher plants [31]. In addition, rice plants accumulate proline, polyamines, and ABA while accumulate lower rubisco thus photochemical efficiency is reduced [10]. Plants develop a sophisticated antioxidant system to counteract the effects of oxidative stress brought on by drought, which aids *O. sativa* to tolerate and resist the effects of drought.

The conclusive figure (Fig. 3) shows the effect of drought stress on the different attributes of rice plants: biochemical, morphological, and physiological traits.

5. Growth stages of rice in response to drought

Drought stress is recognized at various phases of crop growth depending on the sensitivity and variety of the crop. For instance, it was discovered that the percentage of unfilled grains was much higher in places affected by drought during the reproductive stage. It demonstrated rice plants extreme sensitivity to water stress ranging from mild to severe intensity during the reproductive stage (booting, flowering, and panicle initiation) [32]. This effect could be attributed to a decrease in assimilating translocation to reproductive parts [33]. During the vegetative stage, leaf growth and stems, and photosynthesis significantly impact the plant and its overall development [34]. Literature suggests rice is more sensitive to drought during the reproductive phases, such as the blooming stage, filling stage, or maturity, than during the vegetative phases, such as the tillering stage, jointing stage, and so on [27]. Additionally, the yield could be substantially reduced up to 60% if a drought occurs during the blossoming stage [35]. The tendency of a plant to recover from stress only slowly accounts for the decline in the flowering stage. In contrast, the vegetative phase limits the synthesis of carbohydrates for cell division and growth due to stomatal closure, which is thought to be repairable and partially restricts photosynthesis [36]. The principal effects of drought in the vegetative stage are plant degeneration and poor seed germination and seedling stand, which affect the plant's ability to grow and develop appropriately [37]. Furthermore, less than 20% soil wetness strongly influences plant height throughout the booting, flowering, and grain-filling periods [38]. Rehman et al. [33] suggests the stress from the drought led to a decrease in the number of tillers during the vegetative stages. However, stress reduced grain number and weight during the reproductive and grain-filling stages. Thus, a devastating effect of drought occurs on rice, depending on its various growth stages. The yield reduction of rice due to drought at different growth stages is given in Table 1.

5.1. *Impact of drought stress on seed germination and seedling growth*

Timely and optimal germination is the key to improved crop output. Drought stress reduces plant growth, as well impacts on germination. Rice is sensitive to dry conditions in a high degree during germination and the early phases of seedling growth. Drought prevents the seedling to absorb water from the soil, reducing seedling vigor [9]. In addition, the effects of drought stress include altered membrane transport, decreased Adenosine Triphosphate (ATP) generation, and poor seed germination [14]. The main effects of drought stress are stunted growth and aborted germination [15,44,45]. Due to lack of water, severe seedling germination and growth reduction are recorded during drought stress [9]. In contrast to other crops, rice is vulnerable to drought during germination and the early seedling growth stages. The proper soil humidity and temperature are essential for seed germination. Drought stress interferes with water balance, impairs membrane transport, disrupts metabolic processes at the cellular level, and reduces ATP synthesis and respiration, which results in poor seed germination [45].

5.2. *Impact of drought stress on leaf characteristics*

In water-limited conditions, restricted water potential reduces leaf growth [14]. Poor cell development and reduced leaf area in rice are responses to xylem-interrupted water flow, which includes lower turgor pressure due to water shortage [16]. Drought induces changes in the leaf morphology and ultrastructure, including reduced stomata, decrease in leaf size, thick cell walls, cutinization on the leaf surface, and poor conducting system development [3]. Furthermore, conditions of drought stress alter the leaf's ultrastructure and architecture [26]. Due to the restricted water potential during drought stress, leaf growth decreases [21]. The leaf size decreases, with

Table 2
Several adaptations to induce drought tolerance in rice.

Traits	Function	Reference
Proline contents	Highly accumulated under drought	[50]
Sugar contents	Increased under drought	[50]
Starch contents	Increases and protect the plant	[50]
Leaf starch regulation	Improved osmotic stress tolerance	[51]
Spikelet fertility	Improved under drought stress	[52]
Root dragging resistance	Root infiltration into deeper soil layers	[53]
Superior root infiltration capability	To sightsee a larger soil volume	[54]
Membrane stability	Allows the plant leaves to be effective at high temperatures	[55]
Leaf rolling score	Decrease transpiration	[56]
Relative water contents in the leaf	Directs preservation of promising plant water status	[56]
Deeper and thicker roots	To explore a larger soil volume	[57]
Osmotic adjustment	To allow turgor conservation at a low plant water potential	[58]

(***Source:*** modified from Rasheed et al. [25].

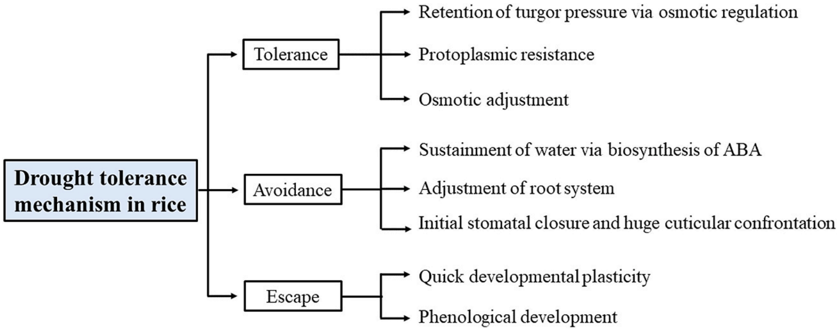

Fig. 4. Plant response to drought stress via avoidance, escape, and tolerance mechanism, showing that the rice plant uses several ways to cope with drought stress, which could be targeted to maintain rice yield under abiotic stress (modified from Rasheed et al. [25]).

fewer stomata, thick cell walls, and cutinization of the leaf surface and the conducting system does not develop as expected. Crop response to disrupted water flow from the xylem to another cell and lower turgor pressure due to water shortage results into poor cell development and reduced leaf area [16]. Other significant traits observed when plants are under drought stress include leaf rolling and the beginning of early senescence [46]. Higher flag leaf area, leaf area index, leaf relative water content, and leaf pigment content are just a few of the leaf features that have been used to screen for drought-tolerant varieties [15,16,19].

One of the key metabolic processes that govern crop growth and yield is photosynthesis, which is impacted by water stress and drought. The typical rate of photosynthesis and the properties of gas exchange in plants are altered by water stress [21]. In the environment with little water, stomata close, lowering the amount of carbon dioxide that reaches the leaves and causing more electrons to be driven toward the creation of ROS [19,20]. Stomatal closure, lowering turgor pressure, decreased leaf gas exchange, and decreased CO_2 uptake are some processes that contribute to the loss of photosynthesis, which ultimately damages the photosynthetic machinery [18,19,21].

5.3. Impact of drought stress on root characteristics

Under drought stress, the morpho-physiological traits of rice roots significantly influence shoot growth and total grain output [47]. Drought can significantly impact root function by changing cell water permeability (hydraulics) and modifying root system growth and architecture. In addition, root dry matter is severely affected by drought stress. Root dry matter typically drops by 5% for vegetative stage dryness, and a comparable response was observed during or after flowering [47]. Due to increased ABA concentration in the roots under drought, rice roots lengthen [48]. In contrast, some studies report a reduction in the root length due to drought stress. Root mass (dry) and length can be used to forecast rice output under water stress [49]. Manivannan et al. [48] noted an increase in the length of rice roots due to an increase in ABA content in the roots. Generally, rice types with a deep and abundant root system are more drought-resistant [47]. This discrepancy in literary works could be due to crop genotypic differences, stress duration, and intensity [47].

Plant root properties are essential for increasing production when facing drought stress. The structure and development of the rice root system affect how a crop performs when faced with water stress. For rice, genotypes with a deep root system, coarse roots, the ability to produce numerous branches, and a high root-to-shoot ratio are crucial for drought resistance [47].

Table 3
Promising drought tolerant genotypes of rice in Nepal and South Asian region.

Name of Variety	Year Released	Country
BRRI dhan56	2011	Bangladesh
BRRI dhan66	2014	Bangladesh
BRRI dhan71	2014	Bangladesh
CR Dhan 201	2014	India
CR Dhan 202	2014	India
DRR Dhan 42	2014	India
DRR Dhan 43	2014	India
Sahbhagi Dhan	2010	India
Sukha Dhan 1	2012	Nepal
Sukha Dhan 2	2012	Nepal
Sukha Dhan 3	2012	Nepal
Sukha Dhan 4	2014	Nepal
Sukha Dhan 5	2014	Nepal
Sukha Dhan 6	2014	Nepal
Hardinath 3	2017	Nepal
Sahod Ulan 23	2016	Philippines
Sahod Ulan 25	2016	Philippines
Katihan 2	2014	Philippines
Katihan 3	2014	Philippines
Yunlu 99	2009	China
RD12 (glutinous)	2007	Thailand
RD33 (non-glutinous)	2007	Thailand

(***Source:*** modified from Majumdar et al. [67], Pray et al. [68] and Luo [69].

6. Adaptations of drought stress in rice

Drought substantially impacts the morphological, physiological, and biochemical pathways of rice plant. The various mechanisms of drought tolerance include genetically regulated cellular changes, physiological acclimation, and morphological adaptations, as illustrated in Table 2. The main metabolic processes that are impeded include photosynthesis, carbon metabolism, and antioxidant defense mechanisms, which are crucial for rice during drought stress. The morphological adaptations include long, thick roots, smaller, lighter leaves, and fewer epithelial cells. Higher stomatal density, a change in internal CO_2 concentration, internal integrity, water-use efficiency, source-to-sink reserve mobilization, a decrease in transpiration rates, lessened and earlier asynchrony between female and male flowering, better production, accumulation, and yield partitioning are all examples of physiological acclimation [59]. High chlorophyll content, lower harvest index and osmotic potential are examples of cellular adaptations [60]. Activation of stress metabolites, a decrease in antioxidative enzymes, ROS, polyamines, osmotic regulation are other biochemical reactions assist in regulating signal transduction and gene expression [59].

7. Drought tolerance mechanism and tolerant genotypes of rice

Drought tolerance, drought escape, drought resistance, and genetic engineering are proper coping mechanisms [61]. Plant response to drought stress via avoidance, escape, and tolerance mechanism as shown in Fig. 4. When a plant completes its life cycle before experiencing severe soil water shortages, the process of 'drought escape' occurs. Early maturing cultivars to avoid the dry season, rapid phenological growth and developmental adaptability enable this approach. With minimal vegetative growth and rapid phenological development, plants can create flowering plants that bear seeds using a small amount of water. However, during their seasons of copious rain, plants can produce many seeds and vegetative growth due to developmental plasticity. Because of this, desert ephemerals may survive and avoid drought [62]. Similarly, drought avoidance describes a plant's capacity to retain a high-water level even without adequate soil moisture. Drought avoidance is the capacity of plants to sustain relatively high tissue water potential despite a lack of soil moisture [61]. This avoidance is accomplished by either increasing soil water content or decreasing water loss. The two primary choices are reducing water loss or preserving water delivery to increase water demand during significant evaporation and developing soil water deficit [59]. It is also listed as one of the mechanisms for resistance to drought [63]. Drought tolerance processes include cellular modifications, physiological acclimation, and morphological adaptations, all governed by genetic variables at various times. For example, cellular adaptations for drought resistance include higher chlorophyll content, decreased osmotic potential, and increased harvest index.

Researchers have previously studied the breeding of drought-tolerant rice genotypes [17,64]. The International Rice Research Institute (IRRI) has conducted most marker-assisted breeding techniques for producing rice varieties that can withstand drought over the past ten years [61,65]. The IRRI has identified several suitable drought-tolerant donors, including PSBRc80, PSBRc68, PSBRc82, Dagaddeshi, AdaySel, Aus 276, Kali Aus, Kalia, Apo, N22, and Dular IR77298-14-1-2, which have been used in numerous intricate conventional and marker-assisted breeding programs to increase grain yield in drought-prone environments. Most high-yielding cultivars, including Swarna, Samba-mahsuri, and IR36, previously suggested for cultivation in irrigated regions, have been adopted in the drought breeding effort. Because the aforementioned high-yielding varieties are resistant to repeated droughts, when grown by

Table 4
QTL for root and shoot characteristics under drought stress.

Plant traits	Mapping population	Marker	Type	Genomic regions	References
Shoot length	M-203 × M-206	SNP	RILs	1	[74]
Shoot dry weight	M-203 × M-206	SNP	RILs	1	[74]
Root parameters	IR1552 × Azucena	SSR	RILs	23	[75]
Deep roots	3 populations	SSR, SNP	RILs	6	[76]
Osmotic adjustment	CT9993 × IR62266	RFLP	DH	5	[77]
Drought avoidance	Bala × Azucena	RFLP	RIL	17	[78]
Grain yield heritability	CT9993 × IR62266	AFLP	DH	1	[79]
Grain yield over localities and years	Apo/2 × Swarna	SSR	RILs	1	[80]
Grain yield under Drought	Two population	SSR	BS	18	[81]
Seedlings drought Tolerance	Indica × Azucena	AFLP and SSR	RILs	7	[82]
Root length and Thickness	IR58821 × IR52561	RFLP	RIL	28	[54]

(***Source:*** Rasheed et al. [25]).

Table 5
QTL associated to drought-related traits in rice.

Traits	QTL	Chr	PVE%	References
Osmotic adjustment	1 (OA70)	8	Major	[58]
Drought avoidance	17	All excluding 9	1.2 to 18.5	[78]
Vegetative stage	*qTWU3-1*	3	9.96	[83]
Leaf area	*qLA3*	3	17.12	[83]
Root traits	264	1–12		[84]
Grain yield under drought stress	1(*qDTY2.3*)	2	9.0	[85]
Plant production	24	1,6	14 to 20.9	[86]
1000-grain weight	21	All except 12	50.3	[87]
Physio-morphological	9	4	36.8	[86]
Grain yield	7	1, 2, 3, 9, 12	31–77	[73]

QTL, Quantitative traits loci: Chr, Chromosome: PVE, Phenotypic Variation Estimate.
(***Source:*** Rasheed et al. [25].

farmers in rainfed ecosystems during the regular drought phase, a considerable decrease in rice output can be observed [66]. More focus is therefore required on developing unique rice varieties with high yields during drought and tolerance to various unfavorable climatic conditions in the future. Some of the most promising drought-tolerant rice genotypes released in Nepal and the South Asian region are listed in Table 3.

8. Breeding for drought tolerance in rice

Genetic engineering and breeding techniques are popular and crucial methods for overcoming drought stress. It is essential to increase drought resistance using traditional breeding techniques [63]. The natural genotypic variation in rice can be studied to find novel genotypes with desirable drought-tolerant features and related genes/loci. Through MAS, these novel genotypes can be used in conventional breeding programs to create drought-tolerant rice varieties. Breeding programs are designed to develop high-yield lines with enhanced quality metrics and then introduce cultivars for agricultural use. The most efficient heterosis breeding technique can enhance yield and associate features governing the proper root growth as a drought-tolerant variety, which help generate rice varieties to perform or overcome drought stress. Like previous techniques, Partial Root-Zone drying (PRD) can sustain the field's water stress [70]. This method of root irrigation wets half of the root system while drying the other, known as a wetting and drying approach. In addition, effective management was used to get through the drought phase and retain the root qualities for good crop performance. This treatment reversed, allowing the previously well-watered side of the root system to dry out while thoroughly irrigating the previously dry side. MAS and genomic selection significantly increases the variety of crop species' capacity to withstand drought directly and indirectly. Similarly, locating donors, mapping Quantitative Trait Locus (QTLs), and marker-assisted breeding can contribute to developing crop-tolerant cultivars [71]. It is possible to choose drought-tolerant genotypes directly depending on how much grain they produce when there is a drought.

Leading rice cultivars have multiple QTLs for drought resistance, including marker-assisted breeding techniques [72,73]. Using a marker-assisted backcrossing technique, researchers successfully included QTLs including qDTY9.1, qDTY2.2, qDTY10.1, and qDTY4.1 in the high-yielding variety IR64 [72,73]. Shamsudin et al. [41] created the Malaysian rice cultivar MR219, which is drought-tolerant, by pyramiding three QTLs: qDTY2.2, qDTY3.1, and qDTY12.1. By incorporating three QTLs, Dixit et al. [64] created the rice variety TDK1 for high production during drought (qDTY3.1, qDTY6.1, and qDTY6.2). QTL for root and shoot characteristics under drought stress is given in Table 4. Drought, the multi-gene controlled quantitative condition, influences the physiological, morphological, and yield-related traits of rice, as illustrated in Table 5. These traits are linked with QTLs, and their genomic region on the chromosome is localized through genomic mapping [88]. It clarifies our understanding of the responsible genes and genetic mechanisms of the variation. Based on thirteen traits of rice, 653 QTLs have already been identified [89]. Thus, identified QTLs can generate highly drought-resistant varieties using molecular-assisted breeding. The majority of findings coincide with osmotic adjustment, root and shoot reaction, hormonal modification, and the response of the whole plant to drought tolerance. Similarly, positive responses of QTLs to grain yield have also been observed through various research studies.

9. Conclusion

Rice under drought stress exhibits lower productivity and has generally slower growth because of poor fertilizer and water uptake. The morphological, physiological, biochemical, and molecular reactions of rice plant are changed by drought stress. It is necessary to implement potential mitigation strategies to improve the population economic and social standing of population. The short-term mitigation options include the selection of drought-tolerant cultivars, planting of early types, and maintaining adequate moisture on the field. The full potential for creating drought-tolerant varieties with high-yielding characteristics is now available through identifying donors, mapping, and using marker-aided breeding of the QTLs and genes affecting performance under stress conditions, conventional breeding, molecular genetics, genomics, and low-cost phenotyping programs for drought resistance. Furthermore, the breeding program for drought resistance must consider the goal of pyramiding multiple pertinent features in a crop because a single trait cannot provide drought resistance on its own. Thus, integrating these innovations and approaches will offer a firm foundation for meeting the current farmers' requirements and assisting in meeting the future demand of farmers in drought-prone areas.

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Data availability statement

Data will be made available on request. No new data were generated.

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References

[1] S. Nahar, J. Kalita, L. Sahoo, B. Tanti, Morphophysiological and molecular effects of drought stress in rice, Ann. Plant Sci. 5 (9) (2016) 1409–1416.
[2] J. Zhang, S. Zhang, M. Cheng, H. Jiang, X. Zhang, C. Peng, X. Lu, M. Zhang, J. Jin, Effect of drought on agronomic traits of rice and wheat: a Meta-Analysis, Int. J. Environ. Res. Public Health 15 (5) (2018) 839.
[3] D. Panda, S.S. Mishra, P.K. Behera, Drought tolerance in rice: focus on recent mechanisms and approaches, Rice Sci. 28 (2) (2021) 119–132.
[4] S. Swain, S.K. Mishra, A. Pandey, Inclusion of groundwater and socio-economic factors for assessing comprehensive drought vulnerability over Narmada River Basin, India: a geospatial approach, Appl. Water Sci. 12 (2022) 14.
[5] M.N. Ndjiondjop, P.W. Wambugu, J.R. Sangare, K. Gnikoua, The effects of drought on rice cultivation in sub-Saharan Africa and its mitigation: a review, Afr. J. Agric. Res. 13 (25) (2018) 1257–1271.
[6] G. Melandri, H. AbdElgawad, D. Riewe, J.A. Hageman, H. Asard, G.T. Beemster, N. Kadam, K. Jagadish, T. Altmann, C. Ruyter-Spira, H. Bouwmeester, Biomarkers for grain yield stability in rice under drought stress, J. Exp. Bot. 71 (2) (2020) 669–683.
[7] M. Kusaka, M. Ohta, T. Fujimura, Contribution of inorganic components to osmotic adjustment and leaf folding for drought tolerance in pearl millet, Physiol. Plantarum 125 (2005) 474–489.
[8] C. Kaya, L. Tuna, D. Higgs, Effect of silicon on plant growth and mineral nutrition of maize under water-stress conditions, J. Plant Nutr. 29 (8) (2006) 1469–1480.
[9] C.S. Vibhuti, K. Bargali, S.S. Bargali, Seed germination and seedling growth parameters of rice (*Oryza sativa* L.) varieties as affected by salt and water stress, Indian J. Agric. Sci. 85 (1) (2015) 102–108.
[10] Y. Oladosu, M.Y. Rafii, C. Samuel, A. Fatai, U. Magaji, I. Kareem, Z.S. Kamarudin, I. Muhammad, K. Kolapo, Drought resistance in rice from conventional to molecular breeding: a review, Int. J. Mol. Sci. 20 (14) (2019).
[11] V. Pandey, A. Shukla, Acclimation and tolerance strategies of rice under drought stress, Rice Sci. 22 (4) (2015) 147–161.
[12] R.A. Richards, Defining selection criteria to improve yield under drought, Plant Growth Regul. 20 (2) (1996) 157–166.
[13] P.K. Dash, R. Rai, V. Rai, S. Pasupalak, Drought induced signaling in rice: delineating canonical and non-canonical pathways, Front. Chem. 6 (2018) 264.
[14] Z.T. Sarvestani, H. Pirdashti, S.A.M.M. Sanavy, H. Balouchi, Study of water stress effects in different growth stages on yield and yield components of different rice (*Oryza sativa* L.) cultivars, Pakistan J. Biol. Sci. 11 (10) (2008) 1303–1309.
[15] S.S. Mishra, D. Panda, Leaf traits and antioxidant defense for drought tolerance during early growth stage in some popular traditional rice landraces from Koraput, India, Rice Sci. 24 (4) (2017) 207–217.
[16] H.A. Hussain, S. Hussain, A. Khaliq, U. Ashraf, S.A. Anjum, S. Men, L. Wang, Chilling and drought stresses in crop plants: implications, cross talk, and potential management opportunities, Front. Plant Science 9 (2018) 393.
[17] S.R. Barik, E. Pandit, S.K. Pradhan, S.P. Mohanty, T. Mohapatra, Genetic mapping of morpho-physiological traits involved during reproductive stage drought tolerance in rice, PLoS One 14 (12) (2019), e0214979.
[18] A. Gupta, A. Rico-Medina, A.I. Caño-Delgado, The physiology of plant responses to drought, Science 368 (6488) (2020) 266–269.
[19] M. Farooq, N. Kobayashi, A. Wahid, O. Ito, S.M. Basra, 6 strategies for producing more rice with less water, Adv. Agron. 101 (4) (2009) 351–388.
[20] S.S. Mishra, P.K. Behera, V. Kumar, S.K. Lenka, D. Panda, Physiological characterization and allelic diversity of selected drought tolerant traditional rice (*Oryza sativa* L.) landraces of Koraput, India, Physiol. Mol. Biol. 24 (6) (2018) 1035–1046.

[21] R. Zhu, F. Wu, S. Zhou, T. Hu, J. Huang, Y. Gao, Cumulative effects of drought–flood abrupt alternation on the photosynthetic characteristics of rice, Environ. Exp. Bot. 169 (2020), 103901.

[22] K.B. Singh, Problems and prospects of stress resistance breeding in chickpea, in: Breeding for Stress Tolerance in Cool- Season Food Legumes, John Wiley U.K, 1993, pp. 17–35.

[23] W. Tezera, V. Mitchel, S.P. Driscul, D.W. Lawlor, Effects of water deficit and its interaction with CO_2 supply on the biochemistry and physiology of photosynthesis in sunflower, Exp. Bot. 53 (2002) 1781–1791.

[24] T.C. Hsiao, Plant Responses to water stress, Annu. Rev. Plant Physiol. 24 (1973) 519–570.

[25] A. Rasheed, M.U. Hassan, M. Aamer, M. Batool, S. Fang, Z. Wu, L.I. Huijie, A critical review on the improvement of drought stress tolerance in rice (*Oryza sativa* L.), Not. Bot. Horti Agrobot. Cluj-Napoca 48 (4) (2020) 1756–1788.

[26] H. Upadhyaya, S.K. Panda, Drought Stress Responses and its Management in Rice, in: In Advances in Rice Research for Abiotic Stress Tolerance, Woodhead Publishing, 2019, pp. 177–200.

[27] M.S. Lum, M.M. Hanafi, Y.M. Rafii, A.S.N. Akmar, Effect of drought stress on growth, proline and antioxidant enzyme activities of upland rice, J. Anim. Plant Sci. 24 (5) (2014) 1487–1493.

[28] A.K. Parida, A.B. Das, Salt tolerance and salinity effects on plants: a review, Ecotoxicol. Environ. Saf. 60 (3) (2005) 324–349.

[29] E. Vranova, V. Breusegem, I. Dirk, Signal transduction during oxidative stress, J. Exp. Bot. 53 (372) (2002) 1227–1236.

[30] J. Pireivatloum, N. Qasimov, H. Maralian, Effect of soul water stress on yield and proline content of four wheat lines, Afr. J. Biotechnol. 9 (2010) 36–40.

[31] M. Laxa, M. Liebthal, W. Telman, K. Chibani, K.J. Dietz, The role of the plant antioxidant system in drought tolerance, Antioxidants (Basel) 8 (4) (2019) 94.

[32] S. Khanal, B. Subedi, A. Bhandari, D.M. Giri, B. Shrestha, P. Neupane, S.M. Shrestha, S.P. Gaire, Screening of different rice genotypes against (*Pyricularia grisea*) Sacc. Natural epidemic condition at seedling stage in Chitwan, Nepal, Adv. Crop Sci. Technol. 4 (231) (2016) 1–6.

[33] M.T. Rehman, M.T. Islam, M.O. Islam, Effect of water stress at different growth stages on yield and yield contributing characters of transplanted a man rice, Pakistan J. Biol. Sci. 5 (2) (2002) 169–172.

[34] R.S. Poethig, Vegetative phase change and shoot maturation in plants, Curr. Top. Dev. Biol. 105 (2013) 125–152.

[35] H. Boonjung, S. Fukai, Effects of soil water deficit at different growth stages on rice growth and yield under upland conditions, Field Crop. Res. 48 (1996) 47–55.

[36] B. Barnabás, K. Jäger, A. Fehér, The effect of drought and heat stress on reproductive processes in cereals, Plant Cell Environ. 31 (1) (2008) 11–38.

[37] X. Yang, B. Wang, L. Chen, L. Li, C. Cao, The different influences of drought stress at the flowering stage on rice physiological traits, grain yield and quality, Sci. Rep. 9 (2019) 3742.

[38] M.T. Islam, M.A. Salam, M. Kauser, Effect of soil water stress at different growth stages of rice on yield components and yield. Mitigation of plant drought stress in a changing climate, Pak. J. Life Sci. 5 (2) (1994) 169–172.

[39] Y.S. Guan, R. Serraj, S.H. Liu, J.L. Xu, J. Ali, W.S. Wang, E. Venus, L.H. Zhu, Z.K. Li, Simultaneously improving yield under drought stress and non-stress conditions: a case study of rice (*Oryza sativa* L.), J. Exp. Bot. 61 (15) (2010) 4145–4156.

[40] A.B. Puteh, A.A. Saragih, M.R. Ismail, M.M.A. Mondal, Chlorophyll fluorescence parameters of cultivated (*Oryza sativa L. ssp. Indica)* and weedy rice (*Oryza sativa L. var. nivara)* genotypes under water stress, Aust. J. Crop. Sci. 7 (9) (2013) 1277–1283.

[41] N.A.A. Shamsudin, B.P. Swamy, W. Ratnam, S. Cruz, M. Teressa, A. Raman, A. Kumar, Marker assisted pyramiding of drought yield QTLs into a popular Malaysian rice cultivar, MR219, BMC Genet. 17 (1) (2016) 1–14.

[42] S. Dixit, A. Singh, A. Kumar, Rice breeding for high grain yield under drought: a strategic solution to a complex problem, Int. J. Agron. 10 (1) (2012) 165–178.

[43] B.P.M. Swamy, N.A.A. Shamsudin, S.N.A. Rahman, R. Mauleon, W. Ratnam, M.T.S. Cruz, A. Kumar, Association mapping of yield and yield-related traits under reproductive stage drought stress in rice (*Oryza sativa L.)*, Rice 10 (2017) 21.

[44] M. Farooq, M. Hussain, A. Wahid, K.H.M. Siddique, Drought Stress in Plants: an Overview, in: Plant Responses to Drought Stress, 2012, pp. 1–33.

[45] N.N. Kadam, A. Tamilselvan, L.M. Lawas, C. Quinones, R.N. Bahuguna, M.J. Thomson, M. Dingkuhn, R. Muthurajan, P.C. Struik, X. Yin, S.K. Jagadish, Genetic control of plasticity in root morphology and anatomy of rice in response to water deficit, Plant Physiol. 174 (4) (2017) 2302–2315.

[46] A.A. Shakeel, X. Xiao-yu, W. Long-chang, F.S. Muhammad, M. Chen, L. Wang, Morphological, physiological and biochemical responses of plants to drought stress, Afr. J. Agric. Res. 6 (9) (2011) 2026–2032.

[47] Y. Kim, Y.S. Chung, E. Lee, P. Tripathi, S. Heo, K.H. Kim, Root response to drought stress in rice (*Oryza sativa* L.), Int. J. Mol. Sci. 21 (4) (2020) 1513.

[48] P. Manivannan, C.A. Jaleel, B. Sankar, A. Kishorekumar, R. Somasundaram, G.M.A. Lakshmanan, R. Panneerselvam, Growth, biochemical modifications and proline metabolism in Helianthus annuus L. as induced by drought stress, Colloids Surf. B Biointerfaces 59 (2) (2007) 141–149.

[49] L.H. Comas, S.R. Becker, V.M.V. Cruz, P.F. Byrne, D.A. Dierig, Root traits contributing to plant productivity under drought, Front. Plant Sci. 4 (2013) 442.

[50] D.C. Dien, T. Mochizuki, T. Yamakawa, Effect of various drought stresses and subsequent recovery on proline, total soluble sugar and starch metabolisms in Rice (*Oryza Sativa L.)* varieties, Plant Prod. Sci. 22 (2019) 530–545.

[51] M. Thalmann, D. Pazmino, D. Seung, D. Horrer, Regulation of leaf starch degradation by abscisic acid is important for osmotic stress tolerance in plants, Plant Cell 28 (8) (2016).

[52] S. Moonmoon, M.D.T. Islam, Effect of drought stress at different growth stages on yield and yield components of six rice (*Oryza Sativ* L.*)* genotypes, Fund. Appl. Agric. 2 (3) (2017) 1.

[53] G. Pantuwan, S. Fukai, M. Cooper, S. Rajatasereekul, J. O'toole, Yield response of rice (*Oryza sativa* L.) genotypes to drought under rainfed lowland: 3. Plant factors contributing to drought resistance, Field Crop. Res. 73 (2002) 181–200.

[54] M. Ali, M. Pathan, J. Zhang, G. Bai, S. Sarkarung, H. Nguyen, Mapping QTLs for root traits in a recombinant inbred population from two indica ecotypes in rice, Theor. Appl. Genet. 101 (2000) 756–766.

[55] J. Tripathy, J. Zhang, S. Robin, T.T. Nguyen, H. Nguyen, QTLs for cell-membrane stability mapped in rice (*Oryza Sativa L.)* under drought stress, Theor. Appl. Genet. 100 (2000) 1197–1202.

[56] B. Courtois, G. McLaren, P. Sinha, K. Prasad, R. Yadav, L. Shen, Mapping QTLs associated with drought avoidance in upland rice, Mol. Breed. 6 (2000) 55–66.

[57] R. Yadav, B. Courtois, N. Huang, G. McLaren, Mapping genes controlling root morphology and root distribution in a doubled-haploid population of rice, Theor. Appl. Genet. 94 (1997) 619–632.

[58] J. Lilley, M. Ludlow, S. McCouch, J. O'Toole, Locating QTL for osmotic adjustment and dehydration tolerance in rice, J. Exp. Bot. 47 (1996) 1427–1436.

[59] V. Ramegowda, U.S. Gill, P.N. Sivalingam, GBF3 transcription factor imparts drought tolerance in Arabidopsis thaliana, Sci. Rep. 7 (2017) 9148.

[60] M. Sahebi, M.M. Hanafi, M.Y. Rafii, T.M.M. Mahmud, P. Azizi, M. Osman, R. Abiri, S. Taheri, N. Kalhori, M. Shabanimofrad, G. Miah, N. Atabaki, Improvement of drought tolerance in rice (*Oryza sativa* L.): genetics, genomic tools, and the WRKY gene family, BioMed Res. Int. 11 (9) (2018).

[61] A. Kumar, S. Basu, V. Ramegowda, A. Pereira, Mechanisms of Drought Tolerance in Rice, Burleigh Dodds Sci. Publ. Ltd, 2017, pp. 131–163.

[62] A. Kumar, J. Bernier, S. Verulkar, H.R. Lafitte, G.N. Atlin, Breeding for drought tolerance: direct selection for yield, response to selection and use of drought-tolerant donors in upland and lowland adapted populations, Field Crop. Res. 107 (2008) 221–231.

[63] S. Singh, S. Prasad, V. Yadav, A. Kumar, B. Jaiswal, A. Kumar, N.A. Khan, D.K. Dwivedi, Effect of drought stress on yield and yield components of rice (*Oryza sativa* L.) genotypes, Int. J. Currrr. Microbiol. Appl. Sci. 7 (2017) 2752–2759.

[64] S. Dixit, A. Singh, N. Sandhu, A. Bhandari, P. Vikram, A. Kumar, Combining drought and submergence tolerance in rice: marker-assisted breeding and QTL combination effects, Mol. Breed. 37 (12) (2017) 1–12.

[65] N. Sandhu, A. Kumar, Bridging the rice yield gaps under drought: QTLs, genes, and their use in breeding programs, Agron 7 (2) (2017) 27.

[66] Z. Hao, V.P. Singh, Y. Xia, Seasonal drought prediction: advances, challenges, and future prospects, Rev. Geophys. 56 (1) (2018) 108–141.

[67] R. Majumdar, S. Sakhale, S. Yadav, A. Hossain, A. Kumar, Molecular breeding for improving drought tolerance in rice: recent progress and future perspectives, in: Molecular Breeding for Rice Abiotic Stress Tolerance and Nutritional quality, 2021, pp. 53–74.

[68] C. Pray, L. Nagarajan, L. Li, J. Huang, R. Hu, K.N. Selvaraj, et al., Potential impact of biotechnology on adaption of agriculture to climate change: the case of drought tolerant rice breeding in Asia, Sustainability 3 (10) (2011) 1723–1741.

[69] L.J. Luo, Breeding for water-saving and drought-resistance rice (WDR) in China, J. Exp. Bot. 61 (13) (2010) 3509–3517.

[70] R. Iqbal, M.A.S. Raza, M. Toleikiene, Partial root-zone drying (PRD), its effect and agricultural significance: a review, Bull. Natl. Res. Cent. 44 (2020) 159.

[71] A. Khan, V. Sovero, D. Gemenet, Genome-assisted breeding for drought resistance, Curr. Genom. 17 (2016) 330–342.

[72] M. Singh, B. Kumar, S. Mehandi, K. Chandra, Effect of drought stress in rice: a review on morphological and physiological characteristics, Biosci. Trends 5 (4) (2016) 261–265.

[73] P.R. Singh, N. Jain, P.K. Singh, M.K. Pandey, K. Sharma, Effect of recurrent selection on drought tolerance and related morpho-physiological traits in bread wheat, PLoS One 11 (6) (2016), 0156869.

[74] Y.T. Yun, H.J. Kim, T.H. Tai, Identification of QTLs controlling seedling traits in temperate japonica rice under different water conditions, Plant Breed. Biotechnol. 7 (2) (2019) 106–122.

[75] B. Zheng, L. Yang, W. Zhang, C. Mao, Y. Wu, K. Yi, P. Wu, Mapping QTLs and candidate genes for rice root traits under different water-supply conditions and comparative analysis across three populations, Theor. Appl. Genet. 107 (2003) 1505–1515.

[76] Q. Lou, L. Chen, H. Mei, H. Wei, F. Feng, P. Wang, H. Xia, T. Li, L. Luo, Quantitative trait locus mapping of deep rooting by linkage and association analysis in rice, J. Exp. Bot. 66 (2015) 4749–4757.

[77] J. Zhang, H. Zheng, A. Aarti, G. Pantuwan, T. Nguyen, J. Tripathy, B.D. Nguyen, Locating genomic regions associated with components of drought resistance in rice: comparative mapping within and across species, Theor. Appl. Genet. 103 (2001) 19–29.

[78] A.H. Price, K. Steele, B. Moore, R. Jones, Upland rice grown in soil-filled chambers and exposed to contrasting water-deficit regimes: II. Mapping quantitative trait loci for root morphology and distribution, Field Crop. Res. 76 (2002) 25–43.

[79] R. Kumar, R. Venuprasad, G. Atlin, Genetic analysis of rainfed lowland rice drought tolerance under naturally occurring stress in eastern India: heritability and QTL effects, Field Crop. Res. 103 (2007) 42–52.

[80] R. Venuprasad, C. Dalid, V.M. Del, D. Zhao, M. Espiritu, M.S. Cruz, G. Atlin, Identification and characterization of large-effect quantitative trait loci for grain yield under lowland drought stress in rice using bulk-segregant analysis, Theor. Appl. Genet. 120 (2009) 177–190.

[81] P. Vikram, B.M. Swamy, S. Dixit, H. Ahmed, M.S. Cruz, A.K. Singh, G. Ye, A. Kumar, Bulk segregant analysis: an effective approach for mapping consistent-effect drought grain yield QTLs in rice, Field Crop. Res. 134 (2012) 185–192.

[82] B.S. Zheng, L. Yang, C.Z. Mao, Y.J. Huang, P. Wu, Mapping QTLs for morphological traits under two water supply conditions at the young seedling stage in rice, Plant Sci. 175 (2008) 767–776.

[83] M. Sabar, G. Shabir, S. Masood, S.M. Shah, K. Aslam, S.A. Naveed, M. Arif, Identification and mapping of QTLs associated with drought tolerance traits in rice by a cross between Super Basmati and IR55419-04, Breed Sci. 69 (1) (2019) 169–178.

[84] X. Li, Z. Guo, Y. Lv, X. Cen, X. Ding, H. Wu, X. Li, J. Huang, L. Xiong, Genetic control of the root system in rice under normal and drought stress conditions by genome-wide association study, PLoS Genet. 1 (2017) 24.

[85] A.D. Palanog, B.M. Swamy, N.A.A. Shamsudin, S. Dixit, J.E. Hernandez, T.H. Boromeo, A. Kumar, Grain yield QTLs with consistent-effect under reproductive-stage drought stress in rice, Field Crop. Res. 161 (2014) 46–54.

[86] S.J. Prince, R. Beena, S.M. Gomez, S. Senthivel, R.C. Babu, Mapping consistent rice (*Oryza sativa L.*) yield QTLs under drought stress in target rainfed environments, Rice 8 (2015) 25.

[87] X. Wang, Y. Pang, J. Zhang, Q. Zhang, Y. Tao, B. Feng, Z. Li, Genetic background effects on QTL and QTL× environment interaction for yield and its component traits as revealed by reciprocal introgression lines in rice, The Crop Journal 2 (2014) 345–357.

[88] J. Solis, A. Gutierrez, V. Mangu, E. Sánchez Timm, R. Bedre, S. Linscombe, N. Baisakh, Genetic mapping of quantitative trait loci for grain yield under drought in rice under controlled greenhouse conditions, Front. Chem. 5 (2018) 129.

[89] S. Huang, M. Liu, G. Chen, F. Si, F. Fan, Y. Guo, L. Yuan, F. Yang, S. Li, Favorable QTLs from *Oryza longistaminata* improve rice drought resistance, BMC Plant Biol. 22 (1) (2022) 1–12.